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The restoration of tropical seed dispersal networks

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1 **Author contribution**

2
3 FRS, RRR, MP, JM, DM designed the research; FRS and RF performed the field work; FRS and DM
4 designed analytical methods and analyzed the data; FRS wrote the first draft; all authors contributed
5 substantially to revisions.

6
7 **Abstract:** Human activities have led to the loss of habitats and biodiversity in the Atlantic Rain Forest
8 in Brazil. Ecological restoration aims to rebuild this biome and should include not only the
9 reinstatement of species, but the reestablishment of complex ecological interactions and the ecological
10 functions that they provide. One such function is seed dispersal, which is provided by the interactions
11 between animal frugivores and plants. We studied seed dispersal networks in three different tropical
12 forest sites restored 15, 25 and 57 years ago, temporal scales rarely observed in restoration studies. We
13 investigated changes in network structure (nestedness, modularity and network specialization) in these
14 communities over restoration time. Although network size and the number of interactions increased
15 with time since restoration, the networks were composed of generalist birds, and the large frugivores
16 remained absent. Contrary to our expectations though, species richness was highest in the 25 years old
17 site maybe due the higher number of species used in the planting. Nestedness values were low in all
18 three networks, but the highest nestedness was observed in the intermediate aged site. However, the
19 oldest network was significantly modular and showed higher complementary specialization. These
20 results suggest that, 57 years after restoration, the complexity of mutualistic interactions in seed
21 dispersal networks has increased, this enhancing ecosystem function in the Atlantic forest.

22 **Keywords:** ecosystem function, network structure, seed dispersal, Atlantic forest, birds, restoration
23 age.

1 **Implications for Practice**

- 2 - Restoring the interactions between species is an excellent starting point for rebuilding a community
- 3 structure.
- 4 - Bird-seed dispersal networks can be used as an indicator of restoration of ecosystem function.
- 5 - Measures of network structure could be used as an indicator of restoration success, and frugivorous
- 6 birds can be used as a model for evaluating the influence of restoration in the ecological process in
- 7 fragmented landscapes.

8

9 **Introduction**

10 It is increasingly evident that restoration efforts should focus not only on recovering species diversity
11 and physiognomic traits of the vegetation, but also on the complex ecological interactions involved in
12 the provision of ecosystem functions that ultimately allow ecosystem reconstruction and perpetuation
13 over time (SER 2004; Rodrigues et al. 2009; Devoto et al. 2012). For instance, the re-establishment of
14 mutualistic networks between animal seed dispersers and plants is essential for the long-term
15 ecological restoration of tropical forests, where the majority of plant species rely on animals for seed
16 dispersal (Forup et al. 2008; Devoto et al. 2012). Analyzing the architecture of mutualistic networks
17 between animals and fruit trees in restored areas of forest can provide a useful tool for evaluating and
18 monitoring the restoration of the ecosystem function of seed dispersal (Tylianakis et al. 2010).

19 The Atlantic rainforest is a biodiversity hotspot with high levels of endemism (Myers et al. 2000).
20 Nowadays less than 12% of the original forest remains, distributed mostly in small and isolated
21 fragments (Ribeiro et al. 2009). In 2009, NGOs, governments and research institutions combined forces
22 and started a restoration program called the “Atlantic Forest Restoration Pact” (AFRP,
23 <http://www.pactomataatlantica.org.br/index.aspx?lang=en>) which aims to restore 15 million hectares of
24 degraded land in the Brazilian Atlantic Forest by 2050 (Calmon et al. 2011; Melo et al. 2013).
25 However, whether these restoration actions recover forest communities remains largely unknown and a

1 general limitation of restoration projects worldwide is that monitoring the outcomes of long-term
2 restoration projects is rarely done. The goal of the present study is to analyze restored Atlantic forest
3 sites using a network approach, whereby species and their interactions are recorded and the community
4 is described in terms of community-level properties. To understand changes in network composition
5 and structure following restoration, we studied seed dispersal networks in three different tropical forest
6 sites that were restored 15, 25 and 57 years ago, a time scale which is rarely observed in restoration
7 studies. We used this dataset to address three questions: 1) How does restoration age affect species
8 richness and connectance? Older sites have been available for colonization by species for a longer time,
9 and therefore we expect a positive correlation between restoration age and species richness. Given that
10 connectance is negatively related to network size (Allesina & Tang 2012), we predict a reduction in the
11 connectance of seed dispersal networks following time since restoration; 2) What are the effects of age
12 on the structure of seed dispersal communities? Network structure affects network stability (May 1972;
13 Tylianakis et al. 2010), and network metrics such as nestedness and modularity have been shown to
14 increase community stability (Olesen et al. 2007; Bascompte et al. 2006). Since restoration seeks to
15 increase the stability of restored communities, we predict that the older sites will be more nested and
16 more modular; 3) Does restoration age affect the level of specialization of the seed dispersal
17 community? High specialization is associated with a greater diversity of resources in mutualistic
18 networks, which in turn allows for higher consumer diversity and more coexisting species (Fründ et al.
19 2010). We predict that, with restoration time, more niches will be available and, consequently,
20 communities in older areas will be more specialized.

21

22 **Methods**

23 Study sites are riparian forest areas in the Seasonal Semi-deciduous Forest domain (part of the Atlantic
24 Forest biome) in São Paulo state, Brazil. They were restored by replanting a high plant species
25 diversity (70 to 140 species) 15, 25, and 57 years ago. Both pioneer and non-pioneer species were

1 planted, initially with good weed control (Rodrigues et al. 2009, 2011). Seedlings used in planting were
2 chosen according to availability from commercial sources and also from native seeds collected from the
3 surrounding landscapes. Some alien plants were used and others invaded (e.g. *Cordia alliodora*,
4 *Melia azedarach*, *Callicarpa reevesii*; see species list in Garcia et al. 2014). The 15-yr-old area is 30 ha
5 in size and 1435 m from the nearest forest remnant of comparable size (22°49'43.87"S,
6 47°25'57.71"W). The 25-yr-old area is 50 ha in size and 70 m from nearest fragment (22°34'36.84"S,
7 47°30' 29.92"W), and the 57-yr site is 30 ha in size and 180 m from the nearest fragment
8 (22°40'18.84"S, 47°12'21.64"W; WGS 84) (Garcia et al. 2014) (Fig. 1). All areas are located in a
9 highly degraded landscapes with sugarcane matrixes and low habitat cover.

10

11 Constructing seed-dispersal networks: Sites were sampled from january 2011 to december 2012 at
12 least once a month. At each site, we selected a plot 3 × 1000 meters comprising almost entirely of 1.2
13 km of pre-established trails. Within these plots we collected the data to construct the seed dispersal
14 networks. Within each plot fleshy-fruited plants were tagged and we observed fruit consumption by
15 birds in those plants monthly; we observed every plant that fruited on the plots, though not all tagged
16 plants fruited. We consider all plants with fleshy fruits as potential ornithochorous plants and a species
17 list for each site is provided in the Supporting Information. We built qualitative and quantitative
18 networks for each site, the former being used to calculate modularity and the latter for nestedness and
19 specialization degree. We built both qualitative and quantitative networks because for some feeding
20 observations, the number of fruits consumed was not clear. Qualitative networks were constructed
21 using direct observations of feeding birds made while walking transects through the plots, and also by
22 sampling bird faeces. Five mist nets (3 x 12 meters) were used to capture birds with a sampling effort
23 of 450 hours per site; mist nets were moved around within each plot monthly. Seeds were identified by
24 comparison with reference collection and consultation with specialists. Quantitative networks were
25 constructed using focal-tree observations for 11 tree species totaling 132.4 hours (mean ± SD = 12 ±

1 11.4) in the 15-yr plot, 21 species with 196.1 hours (8.9 ± 6.3) in the 25-yr plot, and 16 species with
2 114.8 hours (7.2 ± 6.2) in the 57-yr plot. In total we undertook 443.3 hours of focal-tree observations.
3 Whenever possible we undertook observations on more than one individual plant per species. We
4 recorded the number of visits, feeding time and number of fruits eaten per visit and we used number of
5 visits to build the quantitative networks. There were differences in species numbers and observation
6 efforts among the three sites due to differences in plant species richness.

7
8 We used null models to determine whether the differences in species richness in the three restored sites
9 were larger than expected by chance. To do this, we assigned to each species a random number
10 between 1 and 900 and then counted how many species fell into three equal-sized classes. These
11 simulations were repeated 1000 times. Then, we plotted the three classes at 95% confidence intervals
12 (CI) to see if the observed differences in species richness are significantly different from random
13 expectations.

14
15 Network descriptors: To characterize the structure of the seed dispersal networks we used descriptors
16 identified as important in establishing the conservation value of ecological networks (connectance,
17 nestedness and modularity; Tylianakis et al. 2010), along with specialization degree which provides an
18 insight on ecosystem functionality (Vazquez et al. 2009; Montoya et al. 2012). Each metric is described
19 below:

20
21 **Connectance**: measures the proportion of realized interactions among the possible ones. Connectance
22 decreases with increasing network size (Jordano 1987).

23
24 **Nestedness**: it has been repeatedly observed that mutualistic networks are often nested, meaning that
25 (i) there is a “core” of generalist species that interact with each other and are responsible for most of

1 the interactions, (ii) specialist species tend to have few interactions and interact preferably with
2 generalist species, and (iii) specialist species rarely interact with each other (Bascompte et al. 2003,
3 2006). This architecture not only minimizes competition and enables more species to coexist (Bastolla
4 et al. 2009; Thébault & Fontaine 2010), but also implies an interaction asymmetry (Bascompte et al.
5 2006) and provides robustness to the random loss of species (Memmott et al. 2004). Evaluating
6 nestedness patterns in restored communities thus reveals aspects of their stability. We calculated
7 nestedness using the index WNODF (Almeida-Neto & Ulrich 2011), which provides a weighted
8 nestedness, measured on scale of 0-100, with high values representing high nestedness.

9
10 **Modularity:** the extent to which species interactions are organized into modules is termed the
11 modularity of the network (Olesen et al. 2007), whereby modules comprise species that are more
12 tightly connected with each other than to species in other modules. Modules are useful for separating
13 functional groups and guilds (Guimerà & Amaral 2005; Mello et al. 2011), and as such they provide
14 information on which species are likely to be important for network function in restored ecosystems
15 (Krause et al. 2003; Teng & McCann 2004). Furthermore, modular networks are considered more
16 stable as they can retain the impacts of a perturbation (e.g., species extinction) within a single module
17 and thereby minimize impacts on other modules (Krause et al. 2003; Teng & McCann 2004).
18 Moreover, it has been suggested that the restoration of modules may be a more successful approach
19 than restoring individual species (Corbet 2000).

20 Modularity (M) was quantified with the software Netcarto (Guimerà & Amaral 2005). M varies from 0
21 (no modules) to 1 (totally separated modules). To test whether the restored networks were significantly
22 more modular than expected by random, we generated 100 networks for each restored site based on our
23 three seed dispersal networks (keeping connectance and number of species constant) and compared
24 modularity of these randomly generated networks with the real seed dispersal networks (Olesen et al.
25 2007; Emer et al. 2013). In addition, we calculated each species “functional role” within the networks

(Guimerà & Amaral 2005) by classifying each species according to Olesen et al. (2007) into peripherals, connectors, module hubs, and network hubs. Because connectors and hubs keep communities from breaking apart and initiating cascade extinctions, the identification of species serving as connectors and hubs could provide useful information for restoration practitioners.

Specialization degree: the specialization of seed dispersal communities was measured as complementary specialization ($H2'$, Blüthgen et al. 2006). $H2'$ is a network-level measure of differentiation that describes the exclusiveness of interactions within the network considering the species degree (i.e. how connected a species is) and how these interactions differ among species (Blüthgen & Klein 2010). The index $H2'$ is useful for comparisons across different networks as it is unaffected by community size or sampling intensity (Blüthgen et al. 2006). $H2'$ values range from 0 (all species interacting with the same partner, i.e. low specialization) to 1 (high specialization).

To determine whether the empirical data display patterns that are significantly different from random, we generated 1000 random networks using the *vaznull* model (Dormann et al. 2008), doing this for the network metrics described above. This model is conservative because it preserves marginal totals (i.e. takes account of interaction abundance) and keeps network connectance constant. All analyses, except for modularity, were carried out using the package bipartite in R (Dormann et al. 2008).

Results

We collected 51 plant species and 39 bird species in the three restored sites. The 25-yr old plot had more species than the 15- or 57-yr old ones for both plants and animals (Fig. 2).

1 *Question 1: Does restoration age affect species richness and connectance?*

2 There were differences in species richness (i.e. network size) among the restored sites (Fig. 3). There
3 were 34 (15 plants + 19 birds), 63 (31 plants + 32 birds), and 33 (16 plants + 17 birds) species in the
4 15, 25 and 57 yr-old plot, respectively. The number of species in the 25-yr-old plot was significantly
5 different from random (95% confidence interval = 21-37).

6
7 Although network complexity increased with time since restoration at all sites, in terms of number of
8 species and interactions, only generalist birds (i.e. species that eat many different kinds of food and
9 utilize forest and others habitats with trees) were recorded. Obligate frugivores (i.e., species that rely
10 heavily upon fruits and normally are strongly associated with closed forest habitats; Snow 1981), as
11 well as large fruit-eating birds such as guans, chachalacas, aracarís and cotingas were absent from all
12 three sites. The largest bird found in the 15- and 25-year sites was the pale-breasted thrush (*Turdus*
13 *leucomelas*, Turdidae). In the 57-year plot we had a single record of a large frugivore, the toucan
14 (*Ramphastos toco*, Ramphastidae). Most of the interactions were made by small frugivores belonging
15 to Turdidae and Thraupidae families.

16
17 Each plant species interacted on average with 2.7 ± 1.7 (mean \pm SD), 4.9 ± 4.7 and 2.5 ± 2.8 birds in
18 the 15-, 25- and 57-yr old sites respectively (Fig. 2). Each bird species interacted on average with $2.7 \pm$
19 2.1 , 4.8 ± 4.8 and 2.65 ± 2.8 plant species in these plots. Only two plant species were found in all three
20 plots (*Cestrum mariquitense*, a shrub in the Solanaceae family, and *Citharexylum myrianthum*, a tree in
21 Verbenaceae family), and there was relatively little overlap in plant species between pairs of plots.
22 Seed dispersers showed higher overlap, with nine species found in all plots and substantial overlap
23 between pairs of plots (Fig. 3). For the quantitative networks, we found 21 (plants + birds = 7 + 14), 47
24 (19 + 27) and 23 (9 + 14) species in 15, 25 and 57 years old sites, respectively. Although there were
25 differences in species richness among plots, there was no difference in connectance between them

1 (0.21, 0.22, and 0.28 for the 15, 25 and 57 years old sites, respectively).

2

3 *Question 2) Does restoration age affect nestedness and modularity of seed dispersal networks?*

4 The networks from the three sites had low nestedness. Contrary to expectation, the highest nestedness
5 value was not observed in the oldest site but in the intermediate-aged site (15 years: WNODF = 13.6, p
6 = 0.006; 25 years: WNODF = 26.9, p = 0.003; 57 years: WNODF = 15.4, p =0.001). In contrast to the
7 older site, the networks from the two younger sites were not modular (M =0.51, p =0.01; Fig. 4). In the
8 older site we found six modules with most links occurring among species within the same module
9 (76.2%, Fig. 4). None of the species in the 57-year network were connectors, but two species (the
10 silver-beaker tanager *Ramphocelus carbo*, and the plant *Trichilia claussoni*) were identified as module
11 hubs. The pale-breasted thrush *Turdus leucomelas* was a network hub, while the remaining bird species
12 were peripherals.

13

14 *3) Does restoration age influence specialization degree?*

15 The specialization degree of the seed dispersal network in the youngest site was not significantly
16 different from random ($H2'$ = 0.51, p = 0.07). However, with the increase in restoration age, the seed
17 dispersal communities begin to show significant differences in specialization from random
18 communities ($H2'$ = 0.3, p = 0.001) in 25 and ($H2'$ = 0.42, p = 0.009) in the 57-yr-old site.

19

20 **Discussion**

21

22 To our knowledge this is the first restoration study that combines long-term restoration with an
23 ecological networks approach. Restoration data becomes scarce or absent beyond 14 years after
24 restoration in the temperate zone (Forup et al. 2008), a pattern probably more accentuated in the
25 tropics. We provide evidence to suggest that active habitat restoration increases network complexity in

1 restored areas of the Atlantic Forest. In line with our expectations, we found a significant increase in
2 modularity and specialization degree in seed dispersal networks with restoration age. Contrary to our
3 expectations though, species richness was highest in the 25-yr-old plot, and nestedness was low in all
4 three networks. In this section we first present the limitations of our study and then discuss our results
5 with respect to our original predictions, ending by considering the use of networks in restoration
6 ecology more generally.

7
8 **Limitations.** The main limitation of this study, and of most restoration studies, is the lack of site
9 replication (Montoya et al. 2012). Although the lack of replication is starting to be addressed in
10 restoration studies, replicated data sets are still rare, and non-existent at long temporal scales even in
11 the Atlantic forest, where the earliest restoration projects started in 1862 but became more common
12 after the 1970s (Rodrigues et al. 2009; Calmon et al. 2011). However, while there are no long-term
13 replicated datasets, decisions still need to be made concerning the best restoration practices in a
14 seriously endangered habitat such as the Atlantic forest. We overcome this limitation to some extent by
15 randomly generating seed dispersal networks at each of the three restored sites and comparing the
16 observed patterns in the network structure of empirical seed dispersal networks versus the patterns
17 observed in 1000 simulated networks with identical species richness and connectance. Therefore, our
18 results provide some much needed insight concerning the likely changes in the structure of mutualistic
19 networks following restoration. A further limitation is the variation in plant species composition among
20 the plots. This is mitigated in part by the fact that complexity is a more a function of richness of
21 species and functional groups, than of individual species composition.

22
23 **The restoration of seed-dispersal networks.** A key finding of this study is that seed dispersal
24 communities became more modular and specialized over time relative to recently restored
25 communities. This is an important result as modular networks are likely to be more stable because they

1 can retain the impacts of a perturbation within a single module and minimize further impacts on other
2 modules (Krause et al. 2003; Teng & McCann 2004; Thébault & Fontaine 2010). Consequently,
3 modularity hinders the propagation of extinctions through the network and increases the robustness of
4 the community (Fortuna et al. 2010; Stouffer & Bascompte 2011).

5 Modular structures are associated with complex communities, which take time to assemble. This is a
6 possible explanation for the lack of modularity in the younger sites. Therefore, the younger sites might
7 be experiencing a period of transient dynamics where complexity has not yet built up again. Another
8 non-exclusive explanation is that different species are found in younger versus older sites, and that
9 species in the younger sites are more generalist (likely after perturbations), thus preventing the
10 formation of modules in the community.

11

12 Modules are also useful for distinguishing different functional groups and guilds (Guimerà & Amaral
13 2005; Mello et al. 2011), and therefore modularity analysis provides information on which species are
14 likely to be important for network function and stability in restored ecosystems. In particular, species
15 serving as connectors and hubs keep communities linked and prevent extinctions (Olesen et al. 2007)
16 and, therefore, the identification of these structurally most important species and their functional roles
17 can provide guidelines for restoration actions. For example, the pale-breasted thrush *Turdus leucomelas*
18 is a network hub in the 57-yr-old network, connecting the six modules present in the community. Aside
19 from the effects on plant reproductive ability, losing this bird species would break the community apart
20 and divide the community into individual modules with fewer species and more vulnerability to
21 perturbations. Restoration projects could use this information and make a particular effort to encourage
22 this bird species in restored sites, for example by planting its favorite food plants (see supporting
23 information), thus accelerating the rebuilding of the mutualistic network. Similarly, looking at the plant
24 species, *Trichilia claussoni* is a module hub (i.e. it is visited by many birds within the same module)
25 and its planting should be strongly encouraged in restored sites to attract birds and recover the seed

1 dispersal network.

2

3 The results reported in this study can also be used to target species relevant for landscape scale
4 restoration, e.g. highly connected bird species like the pale-breasted thrush (*T. leucomelas*), burnished-
5 buff tanager (*Tangara sayaca*), and silver-beaker tanager (*Ramphocelus carbo*). The former two
6 species are able to fly long distances, connecting fragments of forest at the landscape scale and
7 dispersing seeds between them (Pizo & Santos 2011). These are important attributes (Montoya et al.
8 2008), and these bird species are thus fundamental in maintaining habitat connectivity between forest
9 fragments and in ensuring the persistence of bird-dispersed plant species at the landscape scale. The
10 restored sites are located within a highly fragmented landscape where less than 20% of original forest
11 cover remains; this is less than the ideal of 30% original forest cover (Tambosi et al. 2014). While not
12 ideal, this level of forest cover is the reality in our study region and make the restoration of good
13 dispersers particularly important. Similarly, plants that are particularly important to restored
14 communities are *Cestrum mariquitense* (a shrub) and *Citharexylum myrianthum* (a tree), being the only
15 plants found in all three plots. The latter is a highly connected species that produces a high number of
16 fruits and receives a very large number of visits by birds in the three restored communities.

17

18 The 25-yr-old plot supports more bird species than we would expect by chance, and hosts more bird
19 species than the other two sites. This area is close to a natural forest and this is likely to influence its
20 colonization rate along with the fact that it had the highest number of species used during the
21 restoration planting. At this site, the plant species most important for birds in terms of visitation
22 frequency were *Cecropia pachystachya*, a native species, along with *Clausena excavata* and *Callicarpa*
23 *reevesii*, both alien species. The higher richness of birds in the intermediate-aged site could be directly
24 linked to resource (i.e. plants) richness at this site, and the importance of individual plant species to
25 frugivorous birds should be explored in the future.

1
2 Whether or not an alien plant should be used in a restoration project is a contentious point, but one of
3 the practical implications from our results is that different plant species have different values in
4 restoration projects, and choosing the right plants could effectively jump start restoration projects.
5 Ideally, plants with a high value to multiple taxa - not just birds - should be identified. Although the
6 highest bird species richness was seen in the 25-yr-old site, interactions with large frugivorous species
7 – here the toucan, *Ramphastos toco* – was only seen in the 57-yr-old site. Toco toucans are open-
8 country species, rather than forest species and this could have been a chance observation. That said,
9 large frugivores are the key dispersers of large-fruited plant species as they have a larger gape (e.g.
10 Galetti et al. 2013). Furthermore, large frugivore birds disperse seeds over longer distances than small
11 birds, and play a stabilizing role at the landscape/metacommunity scale by connecting habitats in space
12 and time (Lundberg & Mober 2003; Staddon et al. 2010). We observed a low frequency of visitation by
13 toucan (only one visit) and it fed on *Lauraceae* fruits, a family that is characteristic of advanced
14 successional stages. Toucans are a key disperser in Atlantic forest (Galetti et al. 2000), and their
15 absence, together with the absence of other large birds in the more recently restored sites, suggests that
16 there are not enough animals in the landscape for colonization. Another explanation is that the forest
17 does not yet have the right food resources for these large frugivores, a problem that could be addressed
18 by planting of plant species known to be favored by large birds (e.g., *Lauraceae*, *Myristicaceae*; Galetti
19 et al. 2000). Ideally experiments with replicate plots, with and without the addition of these plant
20 families, would be used to determine the key factors important to these bird species.

21 Seed dispersal communities became more specialized over time in our three forests. Because
22 specialization is related with resource complementarity, high levels of specialization mean a high
23 degree of niche differentiation (Blüthgen 2010), and a likely decrease in competition, which facilitates
24 species coexistence (Blüthgen & Klein 2010). Hence the expectation is that as species differ in their
25 functional roles (more complementarity), there is an increase in functionality and biodiversity

1 (Blüthgen & Klein 2010). In keeping with this expectation, we found the 57-yr-old site more
2 specialized (higher $H2'$), suggesting that after five decades of restoration there is an effective increase
3 in ecosystem function in tropical restored forest.

4 The greatest challenge in ecological restoration is to recover stable, fully functional
5 communities. Ecological restoration requires both ecosystem structure and function to be reinstated.
6 This will be particularly challenging when restoring tropical forest given its species richness and
7 complexity. Ecologists and land managers need a better understanding of how network metrics change
8 both as habitats degrade and as they are restored. Indeed, one of the most practical things restoration
9 ecologists and restoration practitioners can do is to establish up long term, replicated study plots for the
10 next generation of restoration ecologists. These experiments need levels of replication suited to both
11 the inherent variability of natural communities and to practical considerations like site loss over the
12 long term. Our results showed that restoration efforts in Atlantic forest are increasing complexity of
13 mutualistic interactions involving seed dispersers and plants, and consequently enhancing ecosystem
14 function in this important threatened biome. Ecological networks provide a powerful tool to evaluate
15 the return of ecosystem functionality and future studies should focus on understanding how this
16 approach can be used to accelerate restoration of tropical forest.

17

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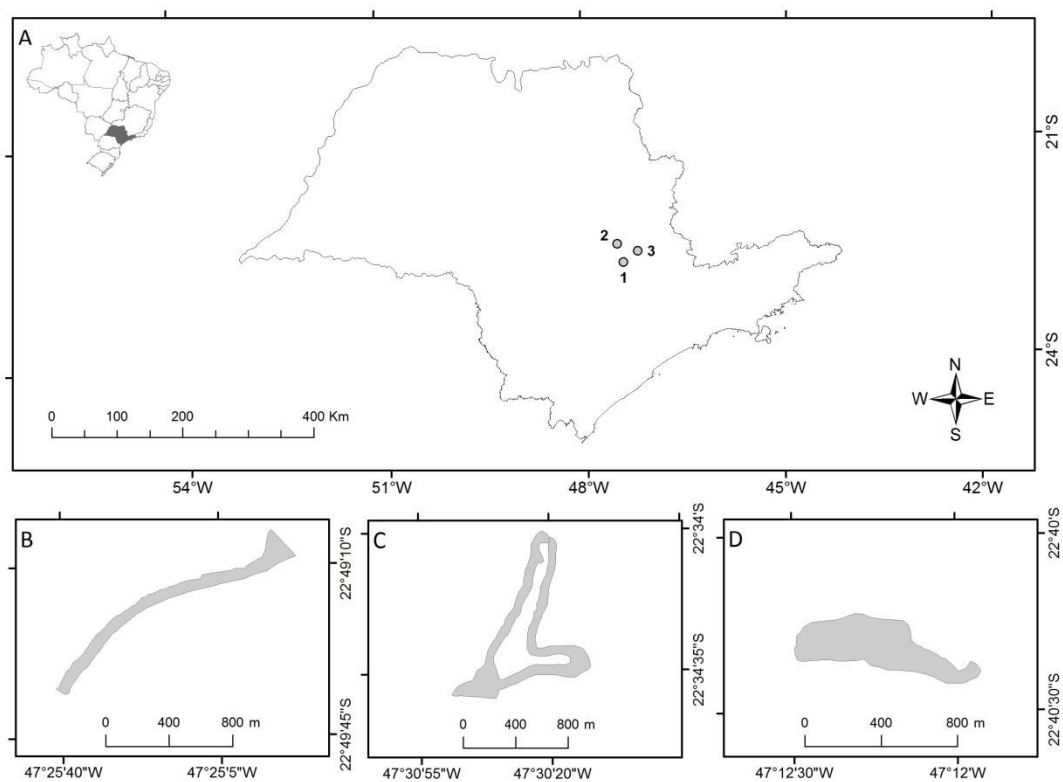
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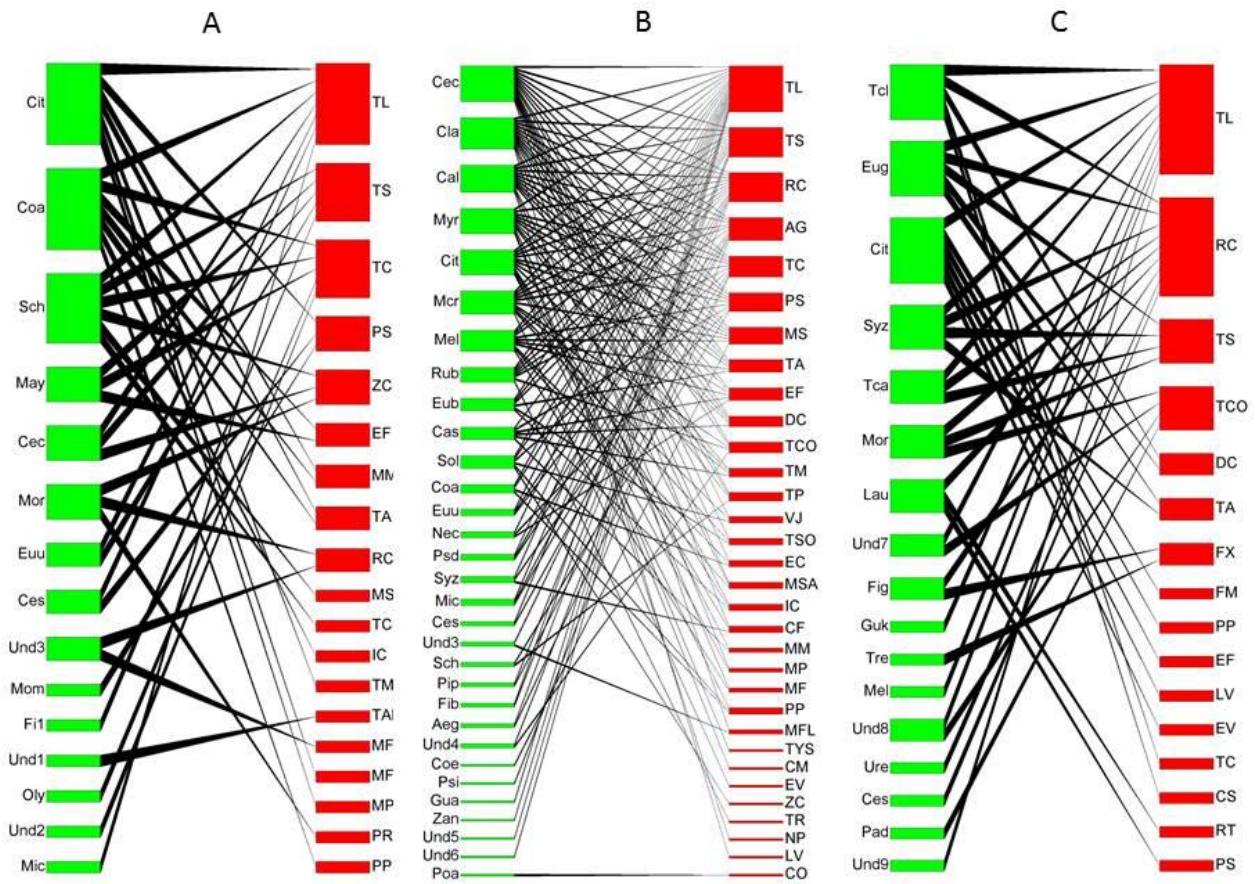
volunteers.

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3 Figure 1. The field site: A) Brazil and São Paulo state; B) 15 year old restored area, in Santa Bárbara
 4 D'Oeste city; C) 25 years old restored area, in Iracemápolis city, D) 57 years old restored area, in
 5 Cosmópolis city.



1 Figure 2. Qualitative bird-seed dispersal networks in three restored sites in São Paulo state, Brazil.
2 The left boxes represent seed species, the right boxes bird species and the links represent the
3 interactions. A) 15 year-old restored plot, B) 25 year-old restored plot, C) 57 year-old plot.

4
5 Bird species: AG-Antilophia galeata; CF-Coereba flaveola; CM- Colaptes melanochloros; CP- Columbina talpacoti; CS-
6 Conirostrum speciosum; DC- Dacnis cayana; EC- Euphonia chlorotica; EF- Elaenia flavogaster; EV- Empidonomus
7 varius; FN- Fluvicola nengeta; FX- Forpus xanthopterygius; IC- Icterus cayanensis; LV- Leptotila verreauxi; MF-
8 Myiarchus ferox; MFL- Myiothlypis flaveola; MM- Myiodynastes maculatus; MP- Megarynchus pitangua; MS- Myiozetetes
9 similis; MSA- Mimus saturninus; NP- Nemosia pileata; PP-Patagioenas picazuro; PR- Pyrrhocomma ruficeps; PS-Pitangus
10 sulphuratus; RC- Ramphocelus carbo; RT- Ramphastos toco; TA-Turdus amaurochalinus; TAL-Turdus albicollis; TC-
11 Tangara cayana; TCO- Tachyphonus coronatus; TL-Turdus leucomelas; TM-Tyrannus melancholicus; TP- Thraupis
12 palmarum; TS-Thraupis sayaca; TSO-Thlypopsis sordida; TYS-Tyrannus savana; VJ- Volatinia jacarina; ZC- Zonotrichia

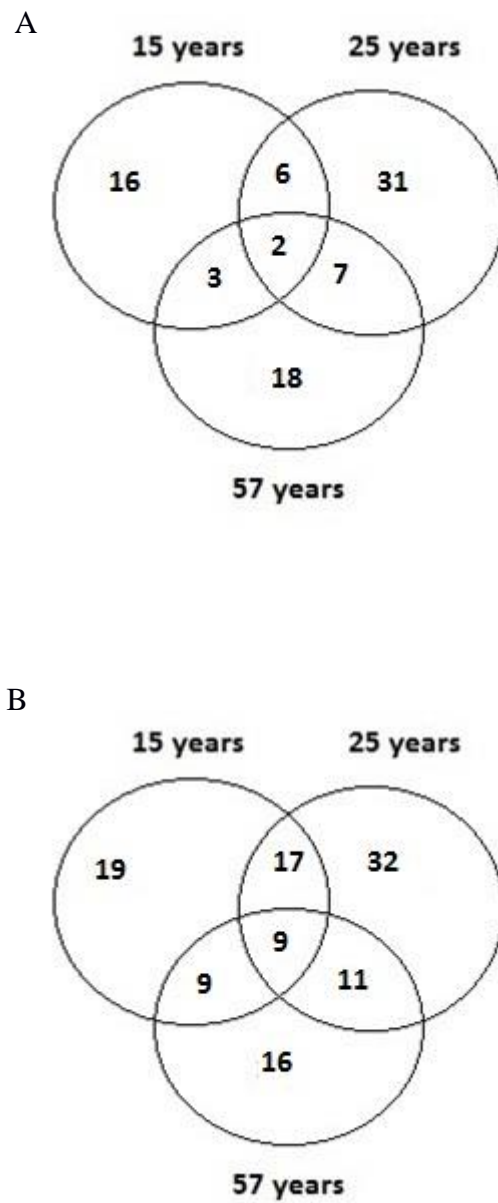
1 *capensis*;
2
3 Plant species: *Aes- Aegiphila sellowiana*; *Cal- Callicarpa reeversi*; *Cas- Casearia sylvestris*; *Cec- Cecropia pachystachya*;
4 *Ces- Cestrum mariquitense*; *Cit- Citharexylum myrianthum*; *Cla- Clausena excavata*; *Coa- Cordia abyssinica*; *Coe-*
5 *Cordia ecalyculata*; *Eub- Eugenia brasiliensis*; *Eug- Eugenia sp1*; *Euu- Eugenia uniflora*; *Fi1-Ficus sp1*; *Fib- Ficus*
6 *benamina*; *Fig- Ficus guaranitica*; *Gua- Guarea sp1*; *Guk- Guarea kunthiana*; *Lau- Lauraceae sp1*; *May- Maytenus*
7 *aquifolia*; *Mel- Melia azedarach*; *Mic- Miconia sp1*; *Mcr- Miconia rubiginosa*; *Mom- Momordica charantia*; *Mor- Morus*
8 *nigra*; *Myr-Myrsine coriacea*; *Nec- Nectandra megapotamica*; *Oly- Olyra sp.*; *Pad- Piper aduncum*; *Pip- Piper sp1*; *Poa-*
9 *Poaceae sp1*; *Psd- Psidium guajava*; *Psi- Psychotria carthagenensis*; *Rub- Rubus rosifolius*; *Sch- Schinus terebinthifolius*;
10 *Sol- Solanum granuloso-leprosum*; *Syz- Syzigium cumini*; *Tca- Trichilia catigua*; *Tcl- Trichilia clauseni*; *Ure- Urera*
11 *baccifera*; *Und- plant specie not determined*; *Zan- Zanthoxylum sp.*

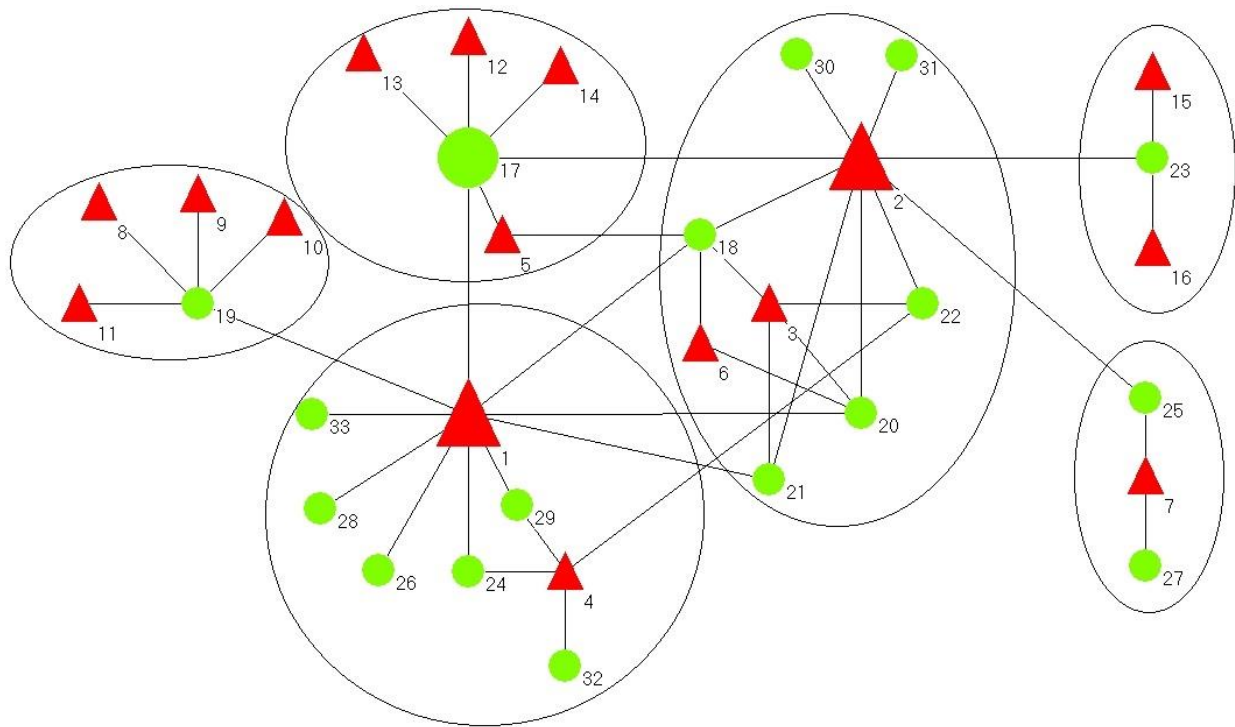
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1 Figure 4. Modules in the seed dispersal network from the 57 year old plot. The network has six
2 modules; in this figure the vertices represent species and links between vertices represent interactions
3 of frugivorous birds. Red triangles represents birds (1-16) and green circles plants (17-33). The larger
4 vertices represent hubs (i.e. species that connected modules, 1-*Turdus leucomelas*) and module hubs (i.
5 e. highly connected species linked to many species within their own module; 2- *Ramphocelus carbo*
6 and 17-*Trichilia claussoni*).

7

8 Birds: 1- *Turdus leucomelas*; 2- *Ramphocelus carbo*; 3- *Thraupis sayaca*; 4- *Tachyphonus coronatus*; 5- *Dacnis cayana*; 6-
9 *Turdus amaurochalinus*; 7- *Forpus xanthopterygius*; 8- *Fluvicola nengeta*; 9- *Patagioenas picazuro*; 10-
10 *Elaenia flavogaster*; 11- *Leptotila verreauxi*; 12- *Empidonomus varius*; 13- *Tangara cayana*; 14- *Conirostrum*
11 *speciosum*; 15- *Ramphastos toco*; 16- *Pitangus sulphuratus*. Plants: 17- *Trichilia claussoni*; 18- *Eugenia sp1*;
12 19- *Citharexylum myrianthum*; 20- *Syzygium cumini*; 21- *Trichilia catigua*; 22- *Morus nigra*; 23- *Lauraceae sp.*;
13 24- *Undetermined 7*; 25- *Ficus guaranitica*; 26- *Guarea kunthiana*; 27- *Trema micrantha*; 28- *Melia azedarach*;
14 29- *Undetermined 8*; 30- *Urera baccifera*; 31- *Cestrum mariquitense*; 32- *Piper aduncum*; 33- *Undetermined 9*.

1 SUPPORTING INFORMATION

2 Table 1. Avian species observed consuming fruits in three restored areas in São Paulo, Brazil. *Alien
3 plant; # naturalized plant. Bird species names follow the checklist of the International Ornithological
4 Congress (available in <http://worldbirdnames.org/names.html>) and plant species names follow APG III
5 (2009).

Birds	Plants	Age since restoration (years)
Columbidae		
<i>Columbina talpacoti</i>	Poaceae sp1	25
<i>Patagioenas picazuro</i>	<i>Citharexylum myrianthum</i> (Verbenaceae)	25, 57
	<i>Solanum granuloso-leprosum</i> (Solanaceae)	25
	<i>Cordia abyssinica</i> * (Boraginaceae)	25
<i>Leptotila verreauxi</i>	<i>Citharexylum myrianthum</i> (Verbenaceae)	57
	<i>Clausena excavata</i> * (Rutaceae)	25
Ramphastidae		
<i>Ramphastos toco</i>	Lauraceae sp1	57
Picidae		
<i>Colaptes melanochloros</i>	<i>Myrsine coriacea</i> (Primulaceae)	25
Psittacidae		
<i>Forpus xanthopterygius</i>	<i>Ficus guaranitica</i> (Moraceae)	57
	<i>Trema micrantha</i> (Cannabaceae)	57
Tyrannidae		
<i>Elaenia flavogaster</i>	<i>Cordia abyssinica</i> * (Boraginaceae)	15
	<i>Maytenus aquifolia</i> (Celastraceae)	15

Birds	Plants	Age since restoration (years)
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
	<i>Citharexylum myrianthum</i> (Verbenaceae)	25, 57
	<i>Melia azedarach</i> (Meliaceae)	25
	<i>Casearia sylvestris</i> (Salicaceae)	25
	<i>Nectandra megapotamica</i> (Lauraceae)	25
<i>Fluvicola nengeta</i>	<i>Citharexylum myrianthum</i> (Verbenaceae)	57
<i>Myiozetetes similis</i>	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
	<i>Myrsine coriacea</i> (Primulaceae)	25
	<i>Citharexylum myrianthum</i> (Verbenaceae)	15, 25
	<i>Miconia rubiginosa</i> (Melastomataceae)	25
<i>Pitangus sulphuratus</i>	<i>Melia azedarach</i> (Meliaceae)	25
	<i>Cordia ecalyculata</i> (Boraginaceae)	25
	<i>Citharexylum myrianthum</i> (Verbenaceae)	15, 25
	<i>Cestrum mariquitense</i> (Solanaceae)	15
	<i>Momordica charantia</i> [#] (Cucurbitaceae)	15
	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Clausena excavata</i> * (Rutaceae)	25

Birds	Plants	Age since restoration (years)
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
	<i>Myrsine coriacea</i> (Primulaceae)	25
	<i>Melia azedarach</i> (Meliaceae)	25
	<i>Casearia sylvestris</i> (Salicaceae)	25
	<i>Nectandra megapotamica</i> (Lauraceae)	25
	<i>Schinus terebinthifolia</i> (Anacardiaceae)	25
	Lauraceae sp1	57
<i>Myiodynastes maculatus</i>	<i>Cordia abyssinica</i> * (Boraginaceae)	15
	<i>Citharexylum myrianthum</i> (Verbenaceae)	15
	<i>Myrsine coriacea</i> (Primulaceae)	25
	<i>Casearia sylvestris</i> (Salicaceae)	25
<i>Megarynychus pitangua</i>	<i>Citharexylum myrianthum</i> (Verbenaceae)	15, 25
	<i>Clausena excavata</i> * (Rutaceae)	25
<i>Empidonomus varius</i>	<i>Miconia rubiginosa</i> (Melastomataceae)	25
	<i>Citharexylum myrianthum</i> (Verbenaceae)	57
<i>Tyrannus melancholicus</i>	<i>Citharexylum myrianthum</i> (Verbenaceae)	15, 25
	<i>Myrsine coriacea</i> (Primulaceae)	25
	<i>Miconia rubiginosa</i> (Melastomataceae)	25
	<i>Casearia sylvestris</i> (Salicaceae)	25
<i>Tyrannus savana</i>	<i>Myrsine coriacea</i> (Primulaceae)	25

Birds	Plants	Age since restoration (years)
<i>Myiarchus ferox</i>	<i>Citharexylum myrianthum</i> (Verbenaceae)	15
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
Pipridae		
<i>Antilophia galeata</i>	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
	<i>Citharexylum myrianthum</i> (Verbenaceae)	25
	<i>Miconia rubiginosa</i> (Melastomataceae)	25
	<i>Rubus rosifolius</i> (Rosaceae)	25
	<i>Eugenia brasiliensis</i> (Myrtaceae)	25
	<i>Eugenia uniflora</i> (Myrtaceae)	25
	<i>Psidium guajava</i> [#] (Myrtaceae)	25
	<i>Miconia</i> sp. (Melastomataceae)	25
	<i>Cestrum mariquitense</i> (Solanaceae)	25
	<i>Psychotria carthagenensis</i> (Rubiaceae)	25
Mimidae		
<i>Mimus saturninus</i>	<i>Schinus terebinthifolia</i> (Anacardiaceae)	15
	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Melia azedarach</i> (Meliaceae)	25

Birds	Plants	Age since restoration (years)
Turdidae		
<i>Turdus leucomelas</i>	<i>Citharexylum myrianthum</i> (Verbenaceae)	15, 25, 57
	<i>Schinus terebinthifolia</i> (Anacardiaceae)	15
	<i>Cordia abyssinica</i> * (Boraginaceae)	15, 25
	<i>Cecropia pachystachya</i> (Urticaceae)	15, 25
	<i>Eugenia uniflora</i> (Myrtaceae)	15, 25
	<i>Cestrum mariquitense</i> (Solanaceae)	15, 25
	<i>Miconia</i> sp. (Melastomataceae)	15, 25
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
	<i>Myrsine coriacea</i> (Primulaceae)	25
	<i>Miconia rubiginosa</i> (Melastomataceae)	25
	<i>Melia azedarach</i> (Meliaceae)	15, 57
	<i>Rubus rosifolius</i> (Rosaceae)	25
	<i>Eugenia brasiliensis</i> (Myrtaceae)	25
	<i>Solanum granuloso-leprosum</i> (Solanaceae)	25
	<i>Nectandra megapotamica</i> (Lauraceae)	25
	<i>Psidium guajava</i> [#] (Myrtaceae)	25
	<i>Syzygium cumini</i> [#] (Myrtaceae)	25, 57
	<i>Cestrum mariquitense</i> (Solanaceae)	15, 25

Birds	Plants	Age since restoration (years)
	<i>Ficus benjamina</i> * (Moraceae)	25
	<i>Guarea kunthiana</i> (Meliaceae)	57
	<i>Zanthoxylum</i> sp1 (Rutaceae)	25
	Undetermined 5 and 6	25
	<i>Trichilia claussoni</i> (Meliaceae)	57
	<i>Eugenia</i> sp. (Myrtaceae)	57
	<i>Trichilia catigua</i> (Meliaceae)	57
	Undetermined 7	57
	<i>Guarea</i> sp1 (Meliaceae)	25
	Undetermined 8	57
	Undetermined 9	57
<i>Turdus amaurochalinus</i>	<i>Citharexylum myrianthum</i> (Verbenaceae)	15
	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
	<i>Myrsine coriacea</i> (Primulaceae)	25
	<i>Melia azedarach</i> (Meliaceae)	25
	<i>Eugenia brasiliensis</i> (Myrtaceae)	25
	<i>Eugenia</i> sp. (Myrtaceae)	57
<i>Turdus albicollis</i>	Undetermined 1	15

Birds	Plants	Age since restoration (years)
Fringillidae		
<i>Euphonia chlorotica</i>	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Melia azedarach</i> (Meliaceae)	25
	<i>Cordia abyssinica</i> * (Boraginaceae)	25
Parulidae		
<i>Myiothlypis flaveola</i>	<i>Cecropia pachystachya</i> (Urticaceae)	25
	Undetermined 5	25
Icteridae		
<i>Icterus cayanensis</i>	<i>Cordia abyssinica</i> * (Boraginaceae)	15
	<i>Citharexylum myrianthum</i> (Verbenaceae)	25
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
	<i>Eugenia brasiliensis</i> (Myrtaceae)	25
Coerebidae		
<i>Coereba flaveola</i>	<i>Citharexylum myrianthum</i> (Verbenaceae)	25
	<i>Cecropia pachystachya</i> Trécul (Urticaceae)	25
	<i>Syzygium cumini</i> [#] (Myrtaceae)	25
Emberezidae		
<i>Zonotrichia capensis</i>	<i>Cecropia pachystachya</i> (Urticaceae)	15
	<i>Morus nigra</i> * (Moraceae)	15
	<i>Solanum granuloso-leprosum</i> (Solanaceae)	25

Birds	Plants	Age since restoration (years)
Thraupidae		
<i>Nemosia pileata</i>	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
	<i>Schinus terebinthifolia</i> (Anacardiaceae)	25
<i>Thlypopsis sordida</i>	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Miconia rubiginosa</i> (Melastomataceae)	25
	<i>Eugenia brasiliensis</i> (Myrtaceae)	25
<i>Pyrrhocomma ruficeps</i>	<i>Morus nigra</i> * (Moraceae)	15
<i>Tachyphonus coronatus</i>	<i>Schinus terebinthifolia</i> (Anacardiaceae)	15
	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Miconia rubiginosa</i> (Melastomataceae)	25
	<i>Rubus rosifolius</i> (Rosaceae)	25
	Undetermined 4, 7 and 9	57
	<i>Morus nigra</i> * (Moraceae)	57
	<i>Piper aduncum</i> (Piperaceae)	57
	<i>Morus nigra</i> * (Moraceae)	57
	Undetermined 3, 4 and 5	25
<i>Ramphocelus carbo</i>	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25

Birds	Plants	Age since restoration (years)
	<i>Schinus terebinthifolia</i> (Anacardiaceae).	
	<i>Myrsine coriacea</i> (Primulaceae)	25
	<i>Citharexylum myrianthum</i> (Verbenaceae)	25
	<i>Miconia rubiginosa</i> (Melastomataceae)	25
	<i>Melia azedarach</i> (Meliaceae)	25
	<i>Rubus rosifolius</i> (Rosaceae)	25
	<i>Eugenia brasiliensis</i> (Myrtaceae)	25
	<i>Eugenia uniflora</i> (Myrtaceae)	25
	<i>Psidium guajava</i> [#] (Myrtaceae)	25
	<i>Miconia</i> sp. (Melastomataceae)	25
	<i>Trichilia clauseni</i> (Meliaceae)	57
	<i>Eugenia</i> sp. (Myrtaceae)	57
	<i>Syzygium cumini</i> [#] (Myrtaceae)	57
	<i>Trichilia catigua</i> (Meliaceae)	57
	<i>Morus nigra</i> [*] (Moraceae)	57
	Lauraceae sp1	57
	<i>Ficus</i> sp1 (Moraceae)	15
	<i>Urera baccifera</i> (Urticaceae)	57
	<i>Cestrum mariquitense</i> (Solanaceae)	57
<i>Thraupis sayaca</i>	<i>Schinus terebinthifolia</i> (Anacardiaceae)	15

Birds	Plants	Age since restoration (years)
	<i>Maytenus aquifolia</i> (Celastraceae)	15
	<i>Cecropia pachystachya</i> (Urticaceae)	15, 25
	<i>Eugenia uniflora</i> (Myrtaceae)	15
	<i>Ficus</i> sp1 (Moraceae)	15
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
	<i>Schinus terebinthifolia</i> (Anacardiaceae).	
	<i>Citharexylum myrianthum</i> (Verbenaceae)	25
	<i>Miconia rubiginosa</i> (Melastomataceae)	25
	<i>Rubus rosifolius</i> (Rosaceae)	25
	<i>Melia azedarach</i> (Meliaceae)	25
	<i>Eugenia brasiliensis</i> (Myrtaceae)	25
	<i>Casearia sylvestris</i> (Salicaceae)	25
	<i>Cordia abyssinica</i> * (Boraginaceae)	25
	<i>Solanum granuloso-leprosum</i> (Solanaceae)	25
	<i>Piper aduncum</i> Piperaceae)	25
	<i>Ficus benjamina</i> * (Moraceae)	25
	<i>Aegiphila sellowiana</i> (Lamiaceae)	25
	<i>Eugenia</i> sp. (Myrtaceae)	57
	<i>Syzygium cumini</i> [#] (Myrtaceae)	57

Birds	Plants	Age since restoration (years)
<i>Thraupis palmarum</i>	<i>Trichilia catigua</i> (Meliaceae)	57
	<i>Morus nigra</i> * (Moraceae)	57
	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Myrsine coriacea</i> (Primulaceae)	25
<i>Tangara cayana</i>	<i>Schinus terebinthifolia</i> (Anacardiaceae)	25
	<i>Schinus terebinthifolia</i> (Anacardiaceae)	15
	<i>Maytenus aquifolia</i> (Celastraceae)	15
	<i>Olyra</i> sp. (Poaceae)	15
	Undetermined 2	15
	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
	<i>Schinus terebinthifolia</i> (Anacardiaceae).	
	<i>Myrsine coriacea</i> (Primulaceae)	25
	<i>Miconia rubiginosa</i> (Melastomataceae)	25
	<i>Rubus rosifolius</i> (Rosaceae)	25
	<i>Solanum granuloso-leprosum</i> (Solanaceae)	25
	<i>Syzygium cumini</i> [#] (Myrtaceae)	25
	<i>Piper aduncum</i> (Piperaceae)	25

Birds	Plants	Age since restoration (years)
<i>Dacnis cayana</i>	<i>Aegiphila sellowiana</i> (Lamiaceae)	25
	<i>Trichilia claussoni</i> (Meliaceae)	25
	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Clausena excavata</i> * (Rutaceae)	25
	<i>Callicarpa reevesii</i> * (Lamiaceae)	25
	<i>Schinus terebinthifolia</i> (Anacardiaceae)	25
	<i>Myrsine coriacea</i> (Primulaceae)	25
	<i>Casearia sylvestris</i> (Salicaceae)	25
	<i>Trichilia claussoni</i> (Meliaceae)	57
<i>Conirostrum speciosum</i>	<i>Eugenia</i> sp (Myrtaceae)	57
	<i>Trichilia claussoni</i> (Meliaceae)	57
<i>Volatinia jacarina</i>	<i>Cecropia pachystachya</i> (Urticaceae)	25
	<i>Miconia rubiginosa</i> (Melastomataceae)	25
	<i>Solanum granuloso-leprosum</i> (Solanaceae)	25